

THE POLYMORPHISM OF ANTS

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THE POLYMORPHISM OF ANTS.*

By WILLIAM MORTON WHEELER.

There is a sense in which the term polymorphism is applicable to all living organisms, since no two of these are ever exactly alike. But when employed in this sense, the term is merely a synonym of "variation," which is the more apt, since polymorphism has an essentially morphological tinge, whereas variation embraces also the psychological, physiological, and ethological differences between organisms. In zoölogy the term polymorphism is progressively restricted, first, to cases in which individuals of the same species may be recognized as constituting two or more groups, or castes, each of which has its own definite characters or complexion. Second, the term is applied only to animals in which these intraspecific groups coexist in space and time and do not arise through metamorphosis or constitute successive generations. Cases of the latter description are referred to "alternation of generations" and "seasonal polymorphism." And third, the intraspecific groups which coincide with the two groups of reproductive individuals in all gonochoristic, or separate-sexed Metazoa are placed in the category of "sex" or "sexual dimorphism." There remain, therefore, as properly representing the phenomena of polymorphism only those animals in which characteristic intraspecific and intrasexual groups of individuals may be recognized, or, in simpler language, those species in which one or both of the sexes appear under two or more distinct forms.

As thus restricted polymorphism is of rare occurrence in the animal kingdom and may be said to occur only in colonial or social species where it is commonly attributed to a physiological division of labor. It attains its clearest expression in the social insects, in some of which, like the termites, we find both sexes equally polymorphic, while in others like the ants, social bees, and wasps, the female alone, with rare exceptions, is differ-

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entiated into distinct castes. This restriction of polymorphism to the female in the social Hymenoptera, with which we are here especially concerned, is easily intelligible if it be traceable, as is usually supposed, to a physiological division of labor, for the colonies of ants, bees, and wasps are essentially more or less permanent families of females, the male representing merely a fertilizing agency temporarily intruding itself on the activities of the community at the moment it becomes necessary to start other colonies. We may say, therefore, that polymorphism among social Hymenoptera is a physical expression of the high degree of social plasticity and efficiency of the female among these insects. This is shown more specifically in two characteristics of this sex, namely the extraordinary intricacy and amplitude of her instincts, which are thoroughly representative of the species, and her ability to reproduce parthenogenetically. This, of course, means a considerable degree of autonomy even in the reproductive sphere. But parthenogenesis, while undoubtedly contributing to the social efficiency of the female, must be regarded and treated as an independent phenomenon, without closer connection with polymorphism, for the ability to develop from unfertilized eggs is an ancient characteristic of the Hymenoptera and many other insects, which made its appearance among the solitary species, like the Tenthredinidæ and Cynipidæ, long before the development of social life. Moreover, polymorphism may occur in male insects which, of course, are not parthenogenetic. That parthenogenesis is intimately connected with sexual dimorphism, at least among the social Hymenoptera, seems to be evident from the fact that the males usually if not always develop from unfertilized, the females from fertilized eggs.

While the bumble-bees and wasps show us incipient stages in the development of polymorphism, the ants as a group, with the exception of a few parasitic genera that have secondarily lost this character, are all completely polymorphic. It is conceivable that the development of different castes in the female may have arisen independently in each of the three groups of the social Hymenoptera, although it is equally probable that they may have inherited a tendency to polymorphism from a common extinct ancestry. On either hypothesis, however, we must admit that the ants have carried the development of the female castes much further than the social bees and wasps, since they have not only produced a wingless form of the worker, in addition to the winged

female, or queen, but in many cases also two distinct castes of workers known as the worker proper and the soldier.

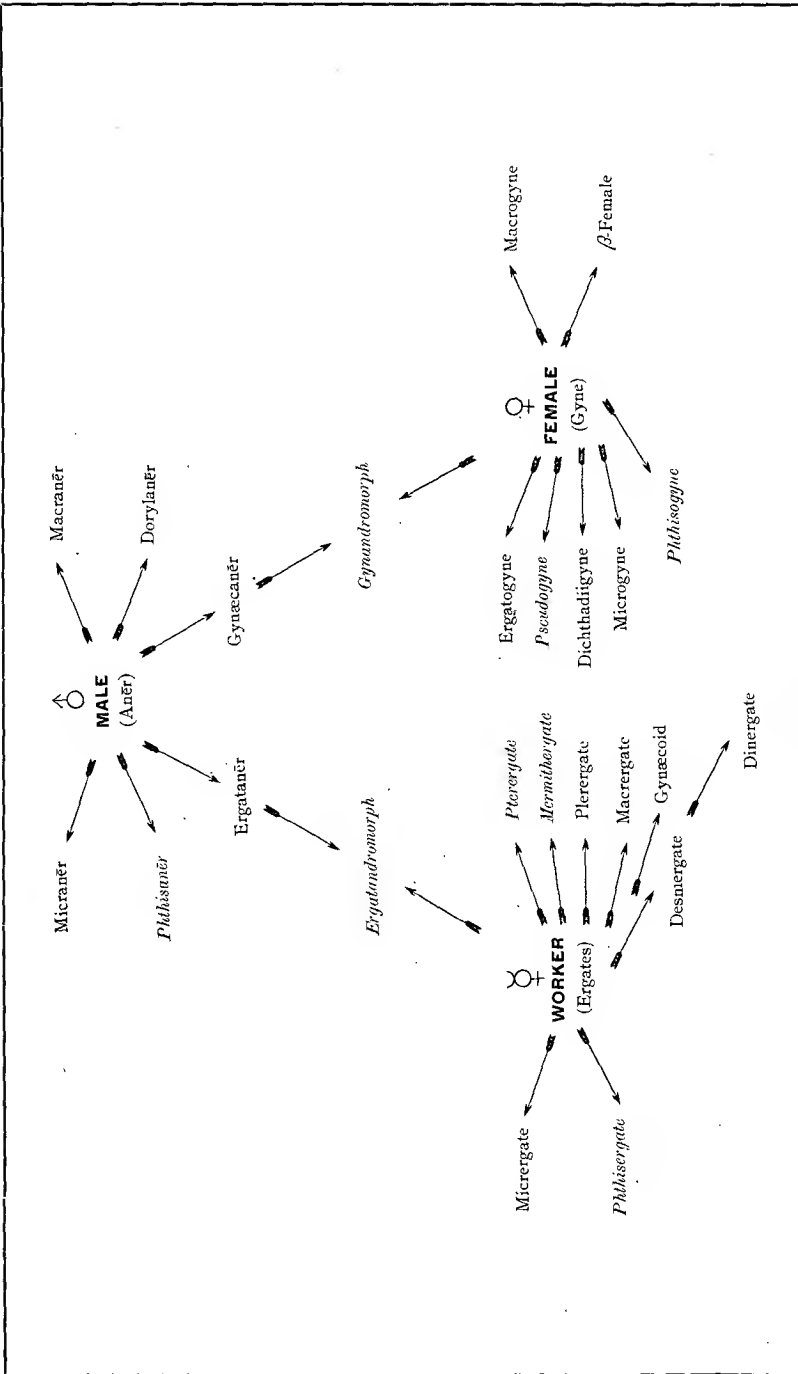
Different authors have framed very different conceptions of the phylogenetic beginnings of social life among the Hymenoptera and consequently also of the phylogenetic origin and development of polymorphism. Thus Herbert Spencer (1893) evidently conceived the colony as having risen from a consociation of adult individuals and although he unfortunately selected a parasitic ant, the amazon (*Polyergus rufescens*), on which to hang his hypothesis, there are a few facts which seem at first sight, to make his view applicable to other social Hymenoptera. Fabre (1894) once found some hundreds of specimens of a solitary wasp (*Ammophila hirsuta*) huddled together under a stone on the summit of Mt. Ventoux in the Provence at an altitude of about 5,500 feet, and Forel (1874) found more than fifty dealated females of *Formica rufa* under similar conditions on the Simplon. I have myself seen collections of a largered and yellow *Ichneumon* under stones on Pike's Peak at an altitude of more than 13,000 feet, and a mass of about seventy dealated females of *Formica gnava* apparently hibernating after the nuptial flight under a stone near Austin, Texas. I am convinced, however, that such congregations are either entirely fortuitous, especially where the insects of one species are very abundant and there are few available stones, or that they are, as in the case of *F. rufa* and *gnava*, merely a manifestation of highly developed social proclivities and not of such proclivities in process of development.

A very different view from that of Spencer is adopted by most authors, who regard the insect society as having arisen, not from a chance concourse of adult individuals but from a natural affiliation of mother and offspring. This view, which has been elaborated by Marshall (1889) among others, presents many advantages over that of Spencer, not the least of which is its agreement with what actually occurs in the founding of the existing colonies of wasps, bumble-bees and ants. These colonies pass through an ontogenetic stage which has all the appearance of repeating the conditions under which colonial life first made its appearance in the phylogenetic history of the species—the solitary mother insect rearing and affiliating her offspring under conditions that would seem to arise naturally from the breeding habits of the nonsocial Hymenoptera. The exceptional methods of colony formation seen in the swarming of the honey bee

and in the temporary and permanent parasitism of certain ants, are too obviously secondary and of too recent a development to require extensive comment. The bond which held mother and daughters together as a community was from the first no other than that which binds human societies together—the bond of hunger and affection. The daughter insects in the primitive colony became dependent organisms as a result of two factors: inadequate nourishment and the ability to pupate very prematurely. But this very ability entailed an incompleteness of imaginal structure and instincts, which in turn must have confirmed the division of labor and thus tended to perfect the social organization.

Before further discussing the problems suggested by this view of the origin of the colony and the general subject of polymorphism it will be advisable to pass in review the series of different phases known to occur among ants. This review will be facilitated by consulting the accompanying diagram, in which I have endeavored to arrange the various phases so as to bring out their morphological relations to one another. The phases may be divided into two main groups, the normal and the pathological. In the diagram the names of the latter are printed in italics. The normal phases may be again divided into primary or typical; and secondary or atypical, the former comprising only the three original phases, male, female, and worker, the latter the remaining phases, which, however, are far from having the same status or frequency. The three typical phases are placed at the angles of an isosceles triangle, the excess developments being placed to the right, the defect developments to the left, of a vertical line passing through the middle of the diagram. The arrows indicate the directions of the affinities of the secondary phases and suggest that those on the sides of the triangle are annectant, whereas those which radiate outward from its angles represent the new departures with excess and defect characters.

(1) The **male** (**aner**) is far and away the most stable of the three typical phases which are found in all but a few monotypic and parasitic genera of ants. This is best shown in the general uniformity of structure and coloration which characterize this sex in genera whose female forms (workers and queens) are widely different; e. g., in such a series as *Myrmecia*, *Odontomachus*, *Cryptocerus*, *Formica*, *Pheidole*, etc. In all of these genera the males are very similar, at least superficially, whereas the



THE TYPICAL, ATYPICAL AND PATHOLOGICAL PHASES OF ANTS.

workers and females are very diverse. The body of the male ant is graceful in form, one might almost say emaciated. Its sense-organs (especially the eyes and antennæ), wings and genitalia are highly developed; its mandibles are more or less imperfectly developed and in correlation with them the head is proportionally shorter, smaller and rounder than in the females and workers of the same species. Even when the latter phases have brilliant or metallic colors, as in certain species of *Macromischa* and *Rhytidoponera*, the males are uniformly red, yellow, brown or black. Yet notwithstanding this monotony of structure and coloration, the male type may present several interesting modifications.

(2) The **macraner** is an unusually large form of male which occasionally occurs in populous colonies.

(3) The **micraner**, or dwarf male, differs from the typical form merely in its smaller stature. Such forms often arise in artificial nests.

(4) The **dorylaner** is an unusually large form peculiar to the driver and legionary ants of the subfamily Dorylinæ (*Dorylus* and *Eciton*). It is characterized by its large and peculiarly modified mandibles, long cylindrical gaster and singular genitalia. It may be regarded as an aberrant macraner that has come to be the typical male of the Dorylinæ.

(5) The **ergataner**, ergatomorphic, or ergatoid male resembles the worker in having no wings and in the structure of the antennæ. It occurs in the genera *Ponera*, *Formicoxenus*, *Symmyrmica* and *Cardiocondyla*. In certain species of *Ponera* (*P. punctatissima* and *ergatandria*) and in *Formicoxenus nitidulus* the head and thorax are surprisingly worker-like, in other forms like *Symmyrmica chamberlini* these parts are more like those of the ordinary male ant, while *P. eduardi* shows an intermediate development of the head with a worker-like thorax. Forel (1904) has recently found that the ergataner may coexist with the aner; at least in one species of *Ponera* (*P. eduardi* Forel). In other words, this ant has dimorphic males.

(6) The **gynæcaner**, or gynæcomorphic male occurs in certain parasitic and workerless genera (*Anergates* and *Epöecus*) and resembles a female rather than a worker form. The male of *Anergates* is wingless, but has the same number of antennal joints as the female. In *Epöecus* both sexes are very much alike and both have 11-12 jointed antennæ (Emery 1906).

(7) The **phthisaner** is a pupal male which in its larval or semi-pupal state has its juices partially exhausted by an Orasema larva. This male is too much depleted to pass on to the imaginal stage. The wings are suppressed and the legs, head, thorax, and antennæ remain abortive.

(8) The **female (gyne)**, or queen, is the more highly specialized sex among ants and is characterized, as a rule, by her larger stature and the more uniform development of her organs. The head is well developed and provided with moderately large eyes, ocelli, and mandibles; the thorax is large (macronotal) and presents all the sclerites of the typical female Hymenopteron; the gaster is voluminous and provided with well developed reproductive organs. The latter possess a receptaculum seminis. The wings and legs are often proportionally smaller than in the male.

(9) The **macrogyne** is a female of unusually large stature.

(10) The **microgyne**, or dwarf female, is an unusually small female which in certain ants, like *Formica microgyna* and its allies, is the only female of the species and may be actually smaller than the largest workers. In other ants, like certain species of *Leptothorax* and *Myrmica*, microgynes may sometimes be found in the same nests as the typical females.

(11) The **β -female** is an aberrant form of female such as occurs in *Lasius laticeps*, either as the only form or coexisting with the normal female, which is then called the α -female. In this case, therefore, the female is dimorphic. The β -female is characterized by excess developments in the legs and antennæ and in the pilosity of the body, or by defective development of the wings.

(12) The **ergatogyne**, ergatomorphic, or ergatoid female, is a worker-like form, with large eyes, ocelli, and a thorax more or less like that of the female, but without wings. Such females occur in a number of species of ants. They have been seen in *Myrmecia*, *Odontomachus*, *Anochetus*, *Ponera*, *Polyergus*, *Leptothorax*, *Monomorium* and *Cremastogaster*. There is nothing to prove that they are pathological in origin. In fact, in *Monomorium floricola*, and certain species of *Anochetus* they appear to be the only existing females. In other cases, like *Ponera eduardi*, as Forel has shown, they occur with more or less regularity in nests with normal workers. They also occur under similar conditions in colonies of the circumpolar *P. coarctata*, and probably also among other species of the genus.

(13) The **pseudogyne** is a worker-like form with enlarged mesonotum and sometimes traces of other thoracic sclerites of the female but without wings or very rarely with wing vestiges. This form occurs in *Formica* colonies infested with parasitic beetles of the genera *Lomechusa* and *Xenodusa*.

(14) The **phthisogyne** arises from a female larva under the same conditions as the phthisaner, and differs from the typical female in the same characters, namely absence of wings, stenonoty, microcephaly and microphthalmy. It is unable to attain to the imaginal instar.

(15) The **worker (ergates)** is characterized by the complete absence of wings and a very small (stenonotal) thorax, much simplified in the structure of its sclerites. The eyes are small and the ocelli are usually absent or, when present, extremely small. The gaster is small owing to the undeveloped condition of the ovaries. A receptaculum seminis is usually lacking, and the number of the ovarian tubules is greatly diminished. The antennæ, legs and mandibles are well developed.

(16) The **gynæcoid** is an egg-laying worker. It is a physiological rather than a morphological phase, since it is probable that all worker ants when abundantly fed become able to lay eggs. Wasmann (1904) observed in colonies of *Formica rufibarbis* that a few workers became gynæcoid and functioned as substitution queens. In colonies of the Ponerine genus *Leptogenys* (including the subgenus *Lobopelta*), and probably also in *Diacamma* and *Champsomyrmex*, the queen phase has disappeared and has been replaced by the gynæcoid worker.

(17) The **dichthadiigyne**, or dichthadiiform female is peculiar to the ants of the subfamily Dorylinæ, and probably represents a further development of the gynæcoid. If this view of the origin of the dichthadiigyne is held, the name of this form in the diagram should be transferred to the worker side. It is wingless and stenonotal, destitute of eyes and ocelli, or with these organs very feebly developed, and with a huge elongated gaster and extraordinary, voluminous ovaries.

(18) The **macrergate** is an unusually large worker form which is sometimes produced in populous or affluent colonies (*Formica*, *Lasius*).

(19) The **micrergate**, or dwarf worker, is a worker of unusually small stature. It appears as a normal or constant form in the first brood of all colonies that are founded by isolated females.

(20) The **dinergate**, or soldier, is characterized by a huge head and mandibles, often adapted to particular functions (fighting and guarding the nest, crushing seeds or hard parts of insects), and a thoracic structure sometimes approaching that of the female in size or in the development of its sclerites (Pheidole).

(21) The **desmergate** is a form intermediate between the typical worker and dinergate, such as we find in more or less isolated genera of all the subfamilies except the Ponerinae, e. g., in Camponotus, some species of Pheidole, Solenopsis, Pogonomyrmex, Azteca, Dorylus, Eciton, etc. The term may also be employed to designate the intermediate forms between the small and large workers in such genera as Monomorium, Formica, etc.

(22) The **plerergate**, "replete", or "rotund," is a worker which in its callow stage has acquired the peculiar habit of distending the gaster with stored liquid food ("honey") till it becomes a large spherical sac and locomotion is rendered difficult or even impossible. This occurs in the honey ants (some North American species of Myrmecocystus, some Australian Melophorus and Camponotus, and in a less extreme form in certain species of Prenolepis and Plagiolepis).

(23) The **pterergate** is a worker or soldier with vestiges of wings on a thorax of the typical ergate or dinergate form, such as occurs in certain species of Myrmica and Cryptocerus.

(24) The **mermithergate** is an enlarged worker, produced by Mermis parasitism and often presenting dinergate characters in the thorax and minute ocelli in the head.

(25) The **phthisergate**, which corresponds to the phthisogyne and phthisaner, is a pupal worker which in its late larval or semi-pupal stage has been attacked and partially exhausted of its juices by an Orasema larva. It is characterized by extreme stenotomy, macrocephaly and microphthalmmy, and is unable to pass on to the imaginal stage. It is in reality an infra-ergatoid form.

(26) The **gynandromorph** is an anomalous individual in which male and female characters are combined in a blended or more often in a mosaic manner.

(27) The **ergatandromorph** is an anomaly similar to the last but having worker instead of female characters combined with those of the male. (Wheeler, 1903.)

It is usually stated that the fertilization or non-fertilization of the egg of the social Hymenopteron determines whether it shall give rise to a male or female. And as the queen represents the

typical female form of the species, the problem of polymorphism is to account for the various worker forms, and those like the soldiers, pseudogynes and ergatoid females which are more or less intermediate between the worker and the queen. The ergatomorphic males are regarded as having inherited worker characters. Thus the problem of polymorphism centers in the development of the worker. It must suffice in this place to give the briefest possible statement of the views of the various authors who have endeavored to account for the development of this caste. These authors may be divided into three groups:

1. Those who believe, with Weismann, that the various castes are represented in the egg by corresponding units (determinants). Fertilization is then regarded as the stimulus which calls the female determinants into activity and meager feeding the stimulus which arouses the worker-producing determinants in the young larvæ arising from fertilized eggs. Such an explanation is obviously little more than a restatement, or "photograph" of the problem. It seeks to account for the adaptive characters of the worker forms through natural selection acting on fortuitous congenital variations.

2. Those who believe, with Herbert Spencer, that there is no such preformation of the various female castes, but that these are produced epigenetically by differences in the feeding of the larvæ. The workers simply arise from larvæ that are inadequately fed but are nevertheless able to pupate and hatch when only a part of their growth has been completed. This is not, like the preceding view, a restatement of the problem, since the modifications induced by inadequate feeding are conceived as somatic and not as germinal, but it fails to explain how the worker caste acquires its adaptive characters, unless this caste is supposed to reproduce with sufficient frequency to transmit acquired somatic modifications to the germ-plasm of the species.

3. A third group of investigators believes, with Emery, that the germ-plasm of the social Hymenopteron is indeed implicated in the phenomenon, not, however, as possessing separate sets of determinants, but as being in a labile or sensitive condition and therefore capable of being deflected along different developmental paths by differences in the trophic stimuli acting on the larva. According to Emery, "the peculiarities in which the workers differ from the corresponding sexual forms are, therefore, not innate or blastogenic; but acquired, that is somatogenic. Nor are they

transmitted as such, but in the form of a peculiarity of the germ-plasm that enables this substance to take different developmental paths during the ontogeny. Such a peculiarity of the germ may be compared with the hereditary predisposition to certain diseases, which like hereditary myopia develop only under certain conditions. The eye of the congenitally myopic individual is blastogenetically predisposed to short-sightedness, but only becomes short-sighted when the accommodation apparatus has been overtaxed by continual exertion. Myopia arises, like the peculiarities of the worker ants, as a somatic affection on a blastogenic foundation.

"With this assumption the problem of the development of workers seems to me to become more intelligible and to be brought a step nearer its solution. The peculiarities of the Hymenopteron workers are laid down in every female egg; those of the termite workers in every egg of either sex, but they can only manifest themselves in the presence of specific vital conditions. In the phylogeny of the various species of ants the worker peculiarities are not transmitted but merely the faculty of all fertilized eggs to be reared as a single or as several kinds of workers. The peculiar instinct of rearing workers is also transmitted since it must be exercised by the fertile females in establishing their colonies."

The views above cited show very clearly that authors have been impressed by very different aspects of the complicated phenomena of polymorphism, and that each has emphasized the aspect which seemed the most promising from the standpoint of the general evolutionary theory he happened to be defending. Escherich (1906) has recently called attention to two very different ways of envisaging the problem; one of these is physiological and ontogenetic, the other ethological and phylogenetic. As these furnish convenient headings under which to continue the discussion of the subject, I shall adopt them, and conclude with a third, the psychological aspect, which is certainly of sufficient importance to deserve consideration.

While the ontogeny of nearly all animals is a repetition or reproduction of the ontogeny of the parent, this is usually not the case in the social Hymenoptera, since the majority of their fertilized eggs do not give rise to queens but to more or less aberrant organisms, the workers. And as these do not, as a rule, reproduce, the whole phenomenon is calculated to arouse the interest of both the physiologist and the embryologist. The former, con-

concentrating his attention on the reactions of the animal to the stimuli proceeding from its environment, is inclined to study its later stages as determined by the reactions to such stimuli, without regard to any internal or hereditary predetermination or disposition, while the embryologist seeks out the earliest moment at which the organism may be shown to deviate from the ontogenetic pattern of its parent. If this moment can be detected very early in the development he will be inclined to project the morphological differentiation back into the germ-plasm and to regard the efforts of the physiologist as relatively unimportant if not altogether futile. Now in his study of the social insects the embryologist is at a serious disadvantage, since he is unable to distinguish any prospective worker or queen characters in the eggs or even in the young larvæ. Compelled, therefore, to restrict his investigations to the older larvæ, whose development as mere processes of histogenesis and metamorphosis throws little or no light on the meaning of polymorphism, he is bound to abdicate and leave the physiologist in possession of the problem.

The physiologist in seeking to determine whether there is in the environment of the developing social Hymenopteron any normal stimulus that may account for the deviation towards the worker or queen type, can hardly overlook one of the most important of all stimuli, the food of the larva. At first sight this bids fair greatly to simplify the problem of polymorphism, for the mere size of the adult insect would seem to be attributable to the quantity, its morphological deviations to the quality of the food administered to it during its larval life. Closer examination of the subject, however, shows that larval alimentation among such highly specialized animals as the social insects, and especially in the honey-bees and ants, where the differences between the queens and workers are most salient, is a subject of considerable complexity. In the first place, it is evident that it is not the food administered that acts as a stimulus but the portion of it that is assimilated by the living tissues of the larva. In other words, the larva is not altogether a passive organism, compelled to utilize all the food that is forced upon it, but an active agent, at least to a certain extent, in determining its own development. And the physiologist might have difficulty in meeting the assertion that the larva utilizes only those portions of the proffered food which are most conducive to the specific predetermined trend of its development. In the second place,

while experiments on many organisms have shown that the quantity of assimilated food may produce great changes in size and stature, there is practically nothing to show that even very great differences in the quality of the food can bring about morphological differences of such magnitude as those which separate the queens and workers of many ants.

These more general considerations are reinforced by the following inferences from the known facts of larval feeding:

1. There seems to be no valid reason for supposing that the morphogeny of the queens among the social Hymenoptera depends on a particular diet, since with the possible exception of the honey and stingless bees, to be considered presently, they differ in no essential respect from the corresponding sexual phase of the solitary species. In both cases they are the normal females of the species and bear the same morphological relations to their males quite irrespective of the nature of their larval food. Hence, with the above mentioned exception, the question of the morphogenic value of the larval food may be restricted to the worker forms.

2. Observation shows that although the food administered to the larvæ of the various social insects is often very different in its nature, even in closely related species, the structure of the workers may be extremely uniform and exhibit only slight specific differences. Ant larvæ are fed with a great variety of substances. The quality of the food itself cannot, therefore, be supposed to have a morphogenic value. And even if we admit what seems to be very probable, namely, that a salivary secretion—possibly containing an enzyme—may be administered by some ants at least to their younger larvæ, the case against the morphogenic effects of qualitative feeding is not materially altered, as we see from the following considerations:

3. In incipient ant-colonies the queen mother takes no food often for as long a period as eight or nine months, and during all this time is compelled to feed her first brood of larvæ exclusively on the secretions of her salivary glands. This diet, which is purely qualitative, though very limited in quantity, produces only workers and these of an extremely small size (micrergates).

4. In the honey-bees, on the other hand, qualitative feeding, namely with a secretion, the so-called "royal jelly," which according to some authors (Schiemenz) is derived from the salivary glands, according to others (Planta) from the chylific stomach of

the nurses, does not produce workers but queens. In this case, however, the food is administered in considerable quantity, and is not provided by a single starving mother, as in the case of the ants, but by a host of vigorous and well-fed nurses. Although it has been taken for granted that the fertilized honey-bee becomes a queen as the result of this peculiar diet, the matter appears in a different light when it is considered in connection with von Ihering's recent observations on the stingless bees (*Meliponidæ*) of South America (1903). He has shown that in the species of *Melipona* the cells in which the males, queens, and workers are reared are all of the same size. These cells are provisioned with the same kind of food (honey and pollen) and an egg is laid in each of them. Thereupon they are sealed up, and although the larvæ are not fed from day to day as in the honey-bees, but like those of the solitary bees subsist on stored provisions, this uniform treatment nevertheless results in the production of three sharply differentiated castes. On hatching the queen *Melipona* has very small ovaries with immature eggs, but in the allied genus *Trigona*, the species of which differ from the *Meliponæ* in constructing large queen cells and in storing them with a greater quantity of honey and pollen, the queen hatches with her ovaries full of ripe eggs. These facts indicate that the large size of the queen cell and its greater store of provisions are merely adaptations for accelerating the development of the ovaries. Now on reverting to the honey-bee we may adopt a similar explanation for the feeding of the queen larva with a special secretion like the "royal jelly." As is well known, the queen honey-bee hatches in about sixteen days from the time the egg is laid, while the worker, though a smaller insect and possessing imperfect ovaries, requires four or five days longer to complete her development. That the special feeding of the queen larva is merely an adaptation for accelerating the development of the ovaries is also indicated by the fact that this insect is able to lay within ten days from the date of hatching. If this interpretation is correct the qualitative feeding of the queen larva is not primarily a morphogenic but a growth stimulus.

5. The grossly mechanical withdrawal by parasites like *Orasema* of food substances already assimilated by the larva, produces changes of the same kind as those which distinguish the worker ant from the queen, i. e., microcephaly, microphthalmia, stenonotia, and aptery. This case is of unusual interest

because the semipupa, after the detachment of the parasite, seems to undergo a kind of regeneration and produces a small but harmonious whole out of the depleted formative substances at its disposal. What is certainly a female or soldier semipupa takes on worker characters while the worker semipupa may be said to become infra-ergatoid as the result of the sudden loss of the formative substances. These observations indicate that the normal worker traits may be the result of starvation or withholding of food rather than of the administration of a particular diet.

6. The pseudogynes of *Formica* admit of a similar interpretation if it be true, as I am inclined to believe, that they arise from starved female larvæ. Here, too, the organism undergoes a kind of regeneration or regulation and assumes the worker aspect owing to a dearth of sufficient formative substances with which to complete the development as originally planned.

7. In the preceding cases the ants take on peculiar structural modifications as the result of tolerating parasites that bring about unusual perturbations in the trophic status of the colony. When ants themselves become parasitic on other ants a similar perturbation ensues, but in these cases the morphological effects are confined to the parasitic species and do not extend to their hosts. This must be attributed to the fact that the parasites live in affluence and are no longer required to take part in the arduous and exacting labors of the colony. Under such circumstances the inhibitory effects of nutritial castration* on the development of the ovaries of the workers are removed and there is a tendency for this caste to be replaced by egg-laying gynæcoid individuals or by ergatogynes, or for it to disappear completely. These effects are clearly visible in nearly all parasitic ants. In the European *Harpegoxenus sublævis*, for example, the only known females in

* Nutritial castration (from *nutrix*, a nurse) as understood by Marchal, must be distinguished from alimentary castration (Emery, *Le Polymorphisme*, etc.), although both are responsible for the infertility of the worker. Through alimentary castration the development of the reproductive organs is inhibited in the larva and pupa, and this inhibition is maintained in the adult by the strong nursing instincts which prevent the workers from appropriating much of the food supply of the colony to their individual use. In many of the higher animals also (birds, mammals) reproduction is inhibited by the exercise of the nutritial function. A third method of inhibiting or destroying the reproductive function is known to occur in the "parasitic castration" of certain bees and wasps (*Andrena*, *Polistes*) by Strepsiptera (*Stylops*, *Xenos*, etc.). See Perez, *Des Effets du Parasitisme des Stylops sur les Apiaries du Genre Andrena*. Actes Soc. Linn. Bordeaux, 1886, 40 pp. 2 pl. Westwood has also described a Strepsipteron (*Myrmecolax nietneri*) which in all probability produces this form of castration in certain Formicidae.

certain localities are gynæcoid workers. In the American *Leptothorax emersoni*, as I have shown (1903), gynæcoid workers and ergatogynes are unusually abundant while the true females seem to be on the verge of disappearing. Among the typical amazon ants (*Polyergus rufescens*) of Europe, ergatogynes are not uncommon. In *Strongylognathus testaceus* the worker caste seems to be dwindling, while in several permanently parasitic genera (*Anergates*, *Wheeleriella*, *Epœcus*, *Epipheidole* and *Sympheidole*) it has completely disappeared. Only one cause can be assigned to these remarkable effects—the abundance of food with which the parasites are provided by their hosts.

8. In the Ponerinæ and certain Myrmicinæ, like Pheidole, *Pogonomyrmex* and *Aphænogaster*, the larvæ are fed on pieces of insects or seeds, the exact assimilative value of which as food can neither be determined nor controlled by the nurses. And while they may perhaps regulate the quantity of food administered, it is more probable that this must fluctuate within limits so wide and indefinite as to fail altogether to account for the uniform and precise morphological results displayed by the personnel of the various colonies. Moreover, any accurate regulation of the food supply by the workers must be quite impossible in cases like that of the *Pachycondyla* larva bearing the commensal *Metopina*.

9. The dependence of the different castes of the social insects on the seasons may also be adduced as evidence of the direct effects of the food supply in producing workers and queens. The latter are reared only when the trophic condition of the colony is most favorable and this coincides with the summer months; in the great majority of species only workers and males are produced at other seasons. Here, too, the cause is to be sought in the deficient quantity of food rather than in its quality, which is, in all probability, the same throughout the year, especially in such ants as the fungus-growing *Attii*.

While these considerations tend to invalidate the supposition that qualitative feeding is responsible for the morphological peculiarities of the worker type, they are less equivocal in regard to the morphogenic effects of quantitative feeding. Indeed several of the observations above cited show very clearly that diminution in stature and, in pathological cases, even reversion to the worker form may be the direct effect of under-feeding. To the same cause we may confidently assign several of the atypical phases among ants, such as the micrergates, microgynes, and micraners, just

as we may regard the macrergates, macrogynes, and macraners as due to overfeeding. These are, of course, cases of nanism and giantism, variations in stature, not in form. Similarly, all cases in which, as in certain species of *Formica*, *Camponotus*, *Pheidole*, etc., the workers or desmergates vary in size, must be regarded as the result of variable quantitative feeding in the larval stage. Here we are confronted with the same conditions as Weismann observed in prematurely pupating blow-flies and entomologists have noticed in many other insects. Such variations are of the fluctuating type and are therefore attributable to the direct effects of the environment. The soldier and worker, however, differ from the queen in the absence of certain characters, like the wings, wing-muscles, spermatheca, some of the ovarian tubules, etc., and the presence of other characters, like the peculiar shape of the head and mandibles. In these respects the sterile castes may be regarded as mutants, and Weismann's contention that such characters cannot be produced by external conditions, such as feeding, is in full accord with De Vries's hypothesis. His further contention, however, that they must therefore be produced by natural selection need not detain us, since it is daily becoming more and more evident that this is not a creative but an eliminative principle. It is certain that very plastic insects, like the ants, have developed a type of ontogeny which enables them not only to pupate at an extremely early period of larval life, but also to hatch and survive as useful though highly specialized members of the colony. It is conceivable that this precocious pupation may be directly responsible for the complete suppression of certain organs that require for their formation more substance than the underfed larva is able to accumulate. At the same time it must be admitted that a direct causal connection between underfeeding on the one hand and the ontogenetic loss or development of characters on the other, has not been satisfactorily established. The conditions in the termites which are often cited as furnishing proof of this connection, are even more complicated and obscure than those of the social Hymenoptera. While Grassi and Sandias (1893) and Silvestri (1901) agree with Spencer in regarding feeding as the direct cause of the production of the various castes, Herbst (1901) who has reviewed the work of the former authors, shows that their observations are by no means conclusive; and Heath (1902) makes the following statement in regard to his experiments on Californian termites: "For months I have fed a

large number of termite colonies of all ages, with or without royal pairs, on various kinds and amounts of food—proctodæal food dissected from the workers or in other cases from royal forms, stomodæal food from the same sources, sawdust to which different nutritious ingredients have been added—but in spite of all I cannot feel perfectly sure that I have influenced in any unusual way the growth of a single individual.”

This rather unsatisfactory answer to the question as to whether quantity or quality of food or both, have an ergatogenic value, has led some investigators to seek a solution along more indirect lines. Thus O. Hertwig and Herbst suggest that the morphogenic stimulus may be furnished by some internal secretion of the reproductive organs. This, too, is possible, but owing to our very imperfect knowledge of the internal secretions, even in the higher animals, we are not in a position either to accept or reject this suggestion.

We may conclude, therefore, that while the conception of the worker type as the result of imperfect nutrition is supported by a considerable volume of evidence, we are still unable to understand how this result can take on so highly adaptive a character. Such a concise effect can hardly be due to manifold and fluctuating external causes like nutrition, but must proceed from some more deeply seated cause within the organism itself. Of course, the difficulty here encountered is by no means peculiar to polymorphism; it confronts us at every turn as the all-pervading enigma of living matter.

An intensive study of the structure and habits of ants must inevitably lead to a certain amount of speculation concerning the phylogenetic development of their colonies. That these insects have had communistic habits for ages is clearly indicated by the fact that all of the numerous existing species are eminently social. There can be little doubt, however, that they rose from forms with habits not unlike those we find today in some of the solitary wasps, such as the *Bembecidæ*, or in the remarkable South African bees of the genus *Allodape*. Unlike other solitary wasps, the females of *Bembex* may be said to be incipiently social, since a number of them choose a nesting site in common and, though each has her own burrow, cooperate with one another in driving away intruders. *Bembex* has also taken an important step in the direction of the social wasps not only in surviving the hatching of her larvæ, but also in visiting them from day to day for the purpose of providing them with fresh insect food.

At a very early period the ants and social wasps must have made a further advance when the mother insect succeeded in surviving till after her progeny had completed their development. This seems to have led naturally to a stage in which the young females remained with their mother and reared their progeny in the parental nest, thus constituting a colony of a number of similar females with a common and indiscriminate interest in the brood. This colony, after growing to a certain size, became unstable in the same way as any aggregate of like units, and must soon have shown a differentiation of its members into two classes, one of the individuals devoted to reproduction and another class devoted to alimentation and protection. In this division of labor only the latter class underwent important somatic modification and specialization, while the former retained its primitive and more generalized characters. It is more than probable, as I shall attempt to show in the sequel, that this differentiation was manifested in the sphere of instinct long before it assumed a morphological expression. The social wasps and the bumble-bees are still in this stage of sociogeny. The ants, however, have specialized and refined on these conditions till they have not only a single marked alimentative and protective caste without wings and lacking many other female characters, but in some species two distinct castes with a corresponding further division of labor. In the phylogeny as well as the ontogeny these characters appear as a result of nutritial castration.

If the foregoing considerations be granted the biogenetic law may be said to hold good in the sociogeny of the ants, for the actual ontogenetic development of their colonies conforms not only to the purely conjectural requirements of phylogeny but also to the stages represented by the various extant groups of social insects. It is clear that we cannot include the honey-bee among these groups, since this insect is demonstrably so aberrant that it is difficult to compare it with the other social insects.

Comparison of the different genera and sub-families of ants among themselves shows that some of them have retained a very primitive social organization, and with it a relatively incomplete polymorphism, whereas others have a much more highly developed social life and a greater differentiation of the castes. Such a comparison, coupled with a study of the natural relationships of the various genera as displayed in structure, suggests that the advance from generalized to highly specialized societies

did not follow a single upward course during the phylogeny, but occurred repeatedly and in different phyletic groups. And since the complications of polymorphism kept pace with those of social organizations, we may say that the differentiation of the originally single worker caste into dinergates, or soldiers, on the one hand, and micrergates, or small workers, on the other, has been several times repeated in remotely related genera. In some genera (*Stenamma* sens. str., *Leptothorax*) there are also indications of a lapsing of highly specialized into simpler conditions by a kind of social degeneration. In its extreme form this manifests itself as a suppression of castes and a consequent simplification of polymorphism. Beautiful illustrations of this statement are furnished by the parasitic species that have lost their worker caste. But there are also cases in which the queen caste has been suppressed and its functions usurped by workers (*Leptogenys*).

Not only have these greater changes been effected and fixed during the phylogenetic history of the Formicidæ, but also many subtler differences such as those of stature, coloration, pilosity and sculpture. And although such differences belong to the class of fluctuating variations and are usually supposed to have a greater ontogenetic than phylogenetic significance, they are undoubtedly of great antiquity and must therefore be regarded as more important than many of the minor morphological traits.

Emery was the first to call attention to a number of peculiar phylogenetic stages in the development of stature among ants. (1894). He found by comparison with the male, which is to be regarded as a relatively stable and conservative form, that the conspecific females and workers may vary in stature independently of each other. The following are the stages which he recognized and some additions of my own:

1. In the earliest phylogenetic condition, which is still preserved in the ants of the subfamily Ponerinæ and in certain Myrmiciniæ (*Pseudomyrma*, *Myrmecina*, etc.), the workers are monomorphic and of about the same size as the males and females.

2. The worker becomes highly variable in stature, from large forms (dinergates, or maxima workers) resembling the female, through a series of intermediates (desmergates, or mediæ) to very small forms (minima workers, or micrergates). This condition obtains in the Dorylinæ, some Myrmiciniæ (*Pheidole*, *Pheidologeton*, *Atta*), Camponotiniæ (*Camponotus*) and Dolichoderiniæ (*Azteca*).

3. The worker becomes dimorphic through the disappearance of the desmergates, so that the originally single variable caste is now represented by two, the soldier (dinergate) and worker proper. We find this condition in certain Myrmicinae and Camponotinae (*Cryptocerus*, *Pheidole*, *Acanthomyrmex*, *Colobopsis*, etc.)

4. The soldier of the preceding stage disappears completely, so that the worker caste again becomes monomorphic, but is represented by individuals very much smaller than the female. Such individuals are really micrergates. This condition is seen in certain Myrmicine genera, especially of the tribe Solenopsidii (*Carebara*, *Erebomyrma*, *Diplomorium*, most species of *Solenopsis*, etc.)

5. The worker form disappears completely leaving only the males and females to represent the species, which thus returns to the condition of sexual dimorphism seen in the great majority of insects and other Metazoa. This occurs in the parasitic ants of the genera *Anergates*, *Wheeleriella*, *Epöcus*, *Sympheidole* and *Epipheidole*.

6. In certain species the workers remain stationary while the female increases in size. This is indicated by the fact that the worker and male have approximately the same stature. Such conditions obtain in certain Myrmicinae (*Cremastogaster*), Camponotinae (*Lasius*, *Prenolepis*, *Brachymyrmex*, the North American species of *Myrmecocystus*), and Dolichoderinae (*Iridomyrmex*, *Dorymyrmex*, *Liometopum*).

7. The worker caste remains stationary while the female diminishes in size till it may become even smaller than the large workers. This occurs in certain parasitic species of North America, like *Aphænogaster tennesseensis* among the Myrmicinae, and among the Camponotinae in the species of the *Formica microgyna* group (*F. difficilis*, *nevadensis*, *impexa*, *dakotensis*, *neptacula*).

8. The female phase disappears completely and is replaced by a fertile, or gynæcoid worker form. This occurs in certain Ponerine genera like *Leptogenys* (including the subgenus *Lobopelta*), and probably also in *Diacamma* and *Champsomyrmex*. The conditions in *Acanthostichus* and certain *Cerapachyi* (*Parasyscia peringueyi*) indicate that the dichthadiigynes of the Dorylinae may have arisen from such gynæcoid workers instead of from winged queens.

9. The female shows a differentiation into two forms (α and β females) characterized by differences in the structure of the legs and antennæ, in pilosity and coloration (*Lasius latipes*), or in the length of the wings (macropterous and micropterous females of *L. niger*). The macrocephalic and microcephalic females of *Camponotus abdominalis* and *confusus* described by Emery (1896) may also be regarded as α and β forms. In this series, stages one to five represent changes in the worker caste while the female remains relatively stationary, whereas stages six to nine represent the converse conditions. Stages one to four probably succeeded one another in the order given, but stage five may have arisen either from the first or fourth. The sixth to ninth stages, must of course, be supposed to have developed independently of one another.

The stature differences described in the above paragraphs are in most if not all cases, highly adaptive. This is clearly seen in such forms as the Indo-African *Carebara*, the huge, deeply, colored females of which are more than a thousand times as large as the diminutive, yellow workers. This ant dwells in termite nests where it occupies chambers connected by means of tenuous galleries with the spacious apartments of its host. The termites constitute a supply of food so abundant and accessible that the workers are able to rear enormous males and females, while they themselves must preserve their diminutive stature in adaptation to their clandestine and thievish habits. Similar conditions are found in many species of the allied genus *Solenopsis*, which inhabit delicate galleries communicating with the nests of other ants on whose larvæ and pupæ they feed. In one species of this genus (*S. geminata*), however, which leads an independent life and feeds on miscellaneous insects and seeds, the worker caste is still highly polymorphic.

Another interesting case of adaptation in stature is seen in the ants of the *Formica microgyna* group. The females of these are temporarily parasitic in the nests of other *Formicæ* and are therefore relieved of the labor of digging nests for themselves and rearing their first brood of larvæ. On this account they need not store up large quantities of food, so that the nourishment which in nonparasitic species goes to produce a comparatively few large females may be applied to the production of a large number of small individuals. This latter condition is, indeed, necessary in parasitic species which are decimated by many

vicissitudes before they can establish themselves successfully among alien hosts. I have already emphasized the adaptive significance of the disappearance of the worker caste among permanently parasitic species like *Anergates*, *Wheeleriella*, etc.

There are several cases in which the worker and female differ greatly in color, pilosity or sculpture, and in such cases either caste may be conservative or aberrant according to ethological requirements. Thus in certain temporary parasites like *Formica ciliata*, *oreas*, *crinita*, *dakotensis*, and *difficilis*, the female is aberrant in one or more of the characters mentioned, while the conspecific worker retains the ancestral characters of the same caste in the closely allied forms of *F. rufa*. The same condition is seen in a very different ant, *Aphænogaster tennesseensis*, as the result of similar parasitic habits. In all of these species the females alone have developed myrmecophilous characters, like the long yellow hairs of *F. ciliata*, or the mimetic coloring of *F. difficilis*, which enable them to foist themselves on allied species and thus avoid the exhausting labor of excavating nests and rearing young, whereas the workers remain unmodified.

The foregoing observations indicate that in morphological characters the worker and female of the same species have advanced or digressed in their phylogeny, remained stationary or retrograded, independently of each other. The same peculiarity is also observable in species with distinct worker and soldier castes. It thus becomes impossible, even in closely related species of certain genera, like *Pheidole*, to predict the characters of the worker from a study of the conspecific soldier or vice versa. And while adaptive characters in stature, sculpture, pilosity and color must depend for their ontogenetic development on the nourishment of the larvæ, it is equally certain that they have been acquired and fixed during the phylogeny of the species. In other words, nourishment, temperature, and other environmental factors merely furnish the conditions for the attainment of characters predetermined by heredity. We are therefore compelled to agree with Weismann that the characters that enable us to differentiate the castes must be somehow represented in the egg. We may grant this however, without accepting his conception of representative units, a conception which has been so often refuted that it is unnecessary to reconsider it in this connection.

Having touched upon this broader problem of heredity it will be necessary to say something about the inheritance or non-inher-

itance of acquired characters, especially as Weismann and his followers regard the social insects as demonstrating the non-transmissibility of somatogenic traits. In establishing this view and the all-sufficiency of natural selection to which it leads, Weismann seems to me to have slurred over the facts. While he admits that the workers may lay eggs, and that these may produce male offspring capable of fertilizing females, he nevertheless insists that this is altogether too infrequent to influence the germ-plasm of the species. I venture to maintain, on the contrary that fertile workers occur much more frequently in all groups of social insects than has been generally supposed. As this fertility is merely a physiological state it has been overlooked. Marchal has shown how readily the workers of the social wasps assume this state, and the same is true of the honey-bees, especially of certain races like the Egyptians and Cyprians (*Apis mellifica*, *fasciata* and *cypria*). In the hives of these insects fertile workers are either always present or make their appearance within a few days after the removal of the queen. Among termites fertile soldiers have been observed by Grassi and Sandias and fertile workers by Silvestri. Among ants fertile, or gynæcoid, workers occur so frequently as to lead to the belief that they must be present in all populous colonies. Their presence is also attested by the production of considerable numbers of males in old and queenless communities. In artificial nests Wasmann, (1891), Miss Fielde (1905) and myself have found egg-laying workers in abundance.

Now as the males that develop from worker eggs are perfectly normal, and in all probability as capable of mating as those derived from the eggs of queens, we are bound to conclude, especially if we adopt the theory of heredity advocated by Weismann himself, that the characters of the mother (in this case the worker) may secure representation in the germ-plasm of the species. Weismann is hardly consistent in denying the probability of such representation, for when he is bent on elaborating the imaginary structure of the germ-plasm he makes this substance singularly retentive of alteration by amphimixis, but when he is looking for facts to support the all-sufficiency of natural selection the germ-plasm becomes remarkably difficult of modification by anything except this eliminative factor. Certainly the simplest and directest method of securing a representation of the worker characters in the germ-plasm would be to get them from the worker itself that has survived in the struggle for existence, rather than through

the action of natural selection on fortuitous constellations of determinants in the germ-plasm of the queen. If we grant the possibility of a periodical influx of worker germ-plasm into that of the species, the transmission of characters acquired by this caste is no more impossible than it is in other animals, and the social insects should no longer be cited as furnishing conclusive proof of Weismannism.

Plate has attempted to overcome the difficulties presented by the normal sterility of the worker by supposing that the distinguishing characters of this caste arose prior to its inability to reproduce. He recognizes the following stages in the phylogeny of the social insects.

"1. The presocial stage with but a single kind of male and female.

"2. The social stage with but a single kind of male and female. The peculiarities in nesting, caring for the brood, and other instincts were already developed during this stage.

"3. The social stage with one kind of male and two or several kinds of females, which were all fertile, but in consequence of the physiological division of labor became more and more different in the course of generations. The division of labor took place in such a manner that the sexual functions passed over primarily to a group A, while the construction of the nest, predatory expeditions and other duties devolved mainly on another group of individuals (B) which on that account used their reproductive organs less and less.

"4. The present stage with one kind of male, a fertile form of female, which arose from group A, and one or several kinds of sterile females, or workers (group B)."

Plate assumes that the differentiation into sterile and fertile forms did not take place till stage 3, and if I understand him correctly, not till after "the races had become differentiated morphologically." This view, as he admits, resembles Spencer's. The two views, in fact differ merely in degree, for the underlying contention is the same, namely that sterility is one of the most recently developed characters among the social insects. There can be little doubt, however, that the smaller adaptive characters, for example those of the females of certain *Formicæ* above mentioned, must have made their appearance in the fourth stage of Plate's scheme. The view which I have advocated differs from Plate's in admitting that even in this stage the workers are fertile

with sufficient frequency to maintain a representation of their characters in the germ-plasm of the species. Conclusive evidence of the presence or absence of such representation can be secured only by experimental breeding and especially by hybridizing the male offspring of workers of one species (a), with females of another (b) that has workers of a different character. Under these conditions some of the characters of (a) should make their appearance in (b).

In the foregoing discussion attention has been repeatedly called to adaptation as the insurmountable obstacle to our every endeavor to explain polymorphism in current physiological terms. Of course, this is by no means a peculiarity of polymorphism, for the same difficulty confronts us in every biological inquiry. As the type of polymorphism with which we are dealing has been developed by psychically highly endowed social insects, it cannot be adequately understood as a mere morphological and physiological manifestation apart from the study of instinct. This has been more or less distinctly perceived by nearly all writers on the subject. However various their explanations, Spencer, Weismann, Emery, Forel, Marchal, and Plate all resort to instinct. Emery, especially, has seen very clearly that a worker type with its peculiar and aberrant characteristics could not have been developed except in a living environment consisting of the fostering queen and workers which instinctively control the development of the young in so far as this depends on external factors. The worker caste may be regarded as a mutation comparable with some of De Vries's *Oenothera* mutations, but able to repeat and maintain itself for an indefinite series of generations in perfect symbiosis with its parent form, the queen, because, notwithstanding its relative infertility, it can be put to very important social use. Among ants this social use not only pervades the activities of the adult workers but extends even to the more inert larval stages. Thus the latter represent a rich and ever-fresh supply of food that can be devoured whenever a temporary famine overtakes the colony. In certain species, like the East Indian *Ecophylla smaragdina* and the South American *Camponotus senex*, the larvæ are put to a more humane use as spinning machines for constructing the silken nest inhabited by the colony. These examples also illustrate the purposive manner in which an organism can satisfy definite needs by taking advantage of ever-present opportunities and mechanisms.

In the lives of the social insects the threptic, or philoprogenerative instincts are of such transcendent importance that all the other instincts of the species, including, of course, those of alimmentation and nest-building, become merely tributary or ancillary. In ants, especially, the instincts relating to the nurture of the young bear the aspect of a dominating obsession. The very strength and scope of these instincts, however, renders the insects more susceptible to the inroads of a host of guests, commensals and parasites. Besides the parasitic larvæ of Chalcidids, Lomechusini and Phorids there are many adult beetles and other insects on which the ants lavish as much or even more attention than they do on their own brood. And when the ants themselves become parasitic on other ants, it is always either for the sake of having their own brood nurtured, as in the temporarily and permanently parasitic forms, or for the purpose of securing the brood of another species, as in the slave-making, or dulotic species.

The philoprogenerative instincts arose and were highly developed among the solitary ancestral insects long before social life made its appearance. In fact, social life is itself merely an extension of these instincts to the adult offspring, and there can be no doubt that once developed it reacted rapidly and powerfully in perfecting these same instincts. It is not so much the fact that all the activities of the social insects converge towards and center in the reproduction of the species, for this is the case with all organisms, as the elaborate living environment developed for the nurture of the young, that gives these insects their unique position among the lower animals. A full analysis of the threptic activities would involve a study of the entire ethology of the social insects and cannot be undertaken at the present time. Nevertheless the bearing of these instincts on the subject of polymorphism can hardly be overestimated and deserves to be emphasized in this connection.

All writers agree in ascribing polymorphism to a physiological division of labor among originally similar organisms. This is tantamount to the assumption that the phylogenetic differentiation of the castes arose in the sphere of function before it manifested itself in structural peculiarities. Although this view implies that the female, or queen, was the source from which both the instincts and structures of the worker were derived, it has been obscured by an improper emphasis on the instincts of the honey-

bee, in which the female is clearly a degenerate organism, and on certain specialized instincts, supposed to belong exclusively to worker ants like those of the slave-makers (*Polyergus*, and *Formica sanguinea*). We have therefore to consider, first the instincts of the queen, and second, any evidence that may go to show that instinct-changes precede morphological differentiation in the phylogeny of the species.

It is evident that the social insects may be divided into two groups according to the instinct role of the queen. In one group, embracing the social wasps, bumble-bees, ants and termites, the female is the complete prototype of her sex. Even the queen of the slave-making ants manifests in the founding of her colonies all the threptic instincts once supposed to be the exclusive prerogative of the worker caste. These may be called the primary instincts. After the colony is established, however, and she no longer needs to manifest these instincts, she becomes a mere egg-laying machine and her instincts undergo a corresponding change and may now be designated as secondary. She thus passes through a gamut of instincts successively called into activity by a series of stimuli which in turn arise in a definite order from her changing social environment. The workers, however, are capable of repeating only a portion of the female gamut, the primary series. In gynæcoid individuals there is also a tendency to take up the secondary series, but in most workers this has been suppressed by countless generations of nutritional castration. The social insects of this type may be called **gynæcotelic**, to indicate that the female has preserved intact the full series of sexual attributes inherited from her solitary ancestors. In these the primary and secondary series were simultaneous or overlapped completely, in the gynæcotelic social insects they are extended over a longer period of time and overlap only in part, as social life permits the extension of the secondary long after the primary series has ceased to manifest itself. It will be seen that the division of labor which led to the special differentiation of like females into workers and queens is clearly foreshadowed in the consecutive differentiation of instincts in the individual queen. The second group of social insects is represented by the honey-bees and probably also by the stingless bees (*Meliponidæ*). In these only the secondary instincts are manifested in the queen, while the worker retains the primary series in full vigor and thus more clearly represents the ancestral female of the species. This type may there-

fore be called **ergatotelic**. The suppression of the primary instincts in the queen honey-bee was undoubtedly brought about by a change in the method of colony formation. When the habit of swarming superseded the establishment of colonies by solitary queens, as still practiced by the gynæcotelic insects, the primary instincts of the female lapsed into abeyance or became latent. This change took place so long ago that it has had time to express itself in the structure of the honey-bee as compared with the worker (shorter tongue and wings, feebler sting, degenerate structure of hind legs, etc.)

The first of the following examples which seem to indicate the occurrence of instinctive prior to morphological differentiation, shows at the same time how the ergatotelic type of the honey-bee may have arisen from the gynæcotelic type of the social wasps and bumble-bees.

1. The queens of certain species of *Formica* (*F. rufa*, *exsectoides*, etc.) are no longer able to establish colonies without the coöperation of workers. The common method of colony formation among these insects is by a process of swarming like that of the honey-bee; a certain portion of the colony emigrates and founds a new nest with one or more of the queens. When this method is impracticable the young queen seeks the assistance of an allied species of *Formica* (*F. fusca*), the workers of which are willing to take the place of her own species in rearing her brood. In *F. rufa* and *exsectoides* there is nothing in the stature or structure of the queen to indicate the presence of these parasitic instincts, but, in many of the allied species, like *F. ciliata*, *dakotensis*, *microgyna*, etc., the colonies of which are smaller and no longer swarm, or do so only to a very limited extent, the queens have become more dependent on the workers of other species and have developed mimetic characters or a dwarf stature to enable them to enter and exploit the colonies of alien *Formicæ*.

2. In many ants the callows, or just-hatched workers, confine themselves to caring for the larvæ and pupæ and do not exhibit the foraging instincts till a later period. But even the adult workers may perform a single duty in the colony for long periods of time, if not indefinitely. Thus Lubbock, (1894), and Viehmeyer (1904) have observed in certain *Formica* colonies that only certain individuals forage for the community. The latter has also noticed that certain individuals, indistinguishable morphologically from their sister workers, stand guard at the nest en-

trances. In other genera, like *Camponotus*, *Atta*, *Pheidole*, etc., with species that have desmergates, the morphological differentiation between foragers and guardians is still unsettled. It becomes completely established, however, in certain genera and species with the suppression of the desmergates. A remarkable example of division of labor without corresponding structural differentiation is seen also in the above mentioned *Cecophylla*, an ant which inhabits a nest of leaves sewn together with fine silk. According to the observations of Dodd (1902) and Doflein (1905), when the nest is torn apart the monomorphic workers separate into two companies, one of which stations itself on the outside, draws the separated leaves together and holds them in place with the claws and mandibles, while the other moves the spinning larvæ back and forth within the nest till the rent is repaired with silken tissue.

3. An interesting case is presented by the honey-ants (*Myrmecocystus melliger* and *mexicanus*.) All the workers of these species, though variable in size, are structurally alike. Among the callows, however, and quite independently of their stature, certain individuals take to storing liquid food, as I have found in my artificial nests of the latter species, and gradually, in the course of a month or six weeks, become repletes, or plerergates. Except for this physiological peculiarity, which slowly takes on a morphological expression, the plerergates and ordinary workers are indistinguishable. We must assume, therefore, that the desire to store food represents an instinct specialization peculiar to a portion of the callow workers. There can be no doubt that as our knowledge of the habits of ants progresses many other cases like the foregoing will be brought to light.

It may be maintained that in these cases physiological states must precede the manifestation of the instincts, and that these states, however inscrutable they may be, are to be conceived as structural differentiations. There is undoubtedly much to justify this point of view. The elaborate sequence of instincts in the queen ant, for example, is accompanied by a series of physiological changes so profound as to be macroscopical. After the loss of her wings, the wing muscles degenerate and the fat-body melts away to furnish nourishment for the ovaries, which, in the old queen, become enormously distended with eggs as the breeding season approaches. Such changes would seem to be amply sufficient to account for the changing instincts. I have found

that mere artificial deaflation at once alters the instincts of the queen, probably through a stimulus analogous to that which leads to the atrophy of a muscle when its nerve is severed, and in the case under consideration leads to the degeneration of the wing-muscles and to changes in the ovaries. In the mermithergates and pseudogynes we also have peculiarities of behavior which are attributable to peculiar physiological states. Similarly, nutricional castration may be said to be a physiological state resembling that of hunger. We may conclude, therefore, that the worker, both in its ontogenetic and phylogenetic development, is through and through a hunger-form, inured to protracted fasting. Miss Fielde has shown (1904) that the workers of *Camponotus americanus* may live nearly nine months without food, which is as long as the much larger and more vigorous queens are known to fast while establishing their colonies. The larvæ of ants, too, are known to remain alive in the nests for months without growing. And even when food is abundant the workers appropriate very little of it to their individual maintenance, but distribute it freely among their sister workers, the brood and queen. It is not improbable, moreover, that the single instinct peculiar to workers, the instinct to leave the nest and forage, is the direct result of a chronic state of hunger.